

Marine protected areas facilitate parasite populations among four fished host species of central Chile

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Summary

1. Parasites comprise a substantial proportion of global biodiversity and exert important ecological influences on hosts, communities and ecosystems, but our knowledge of how parasite populations respond to human impacts is in its infancy.

2. Here, we present the results of a natural experiment in which we used a system of highly successful marine protected areas and matched open-access areas in central Chile to assess the influence of fishing-driven biodiversity loss on parasites of exploited fish and invertebrate hosts. We measured the burden of gill parasites for two reef fishes (*Cheilodactylus variegatus* and *Aplodactylus punctatus*), trematode parasites for a keyhole limpet (*Fissurella latimarginata*), and pinnotherid pea crab parasites for a sea urchin (*Loxechinus albus*). We also measured host density for all four hosts.

3. We found that nearly all parasite species exhibited substantially greater density (# parasites m⁻²) in protected than in open-access areas, but only one parasite species (a gill monogenean of *C. variegatus*) was more abundant within hosts collected from protected relative to open-access areas.

4. These data indicate that fishing can drive declines in parasite abundance at the parasite population level by reducing the availability of habitat and resources for parasites, but less commonly affects the abundance of parasites at the intrapopulation level (within individual hosts).

5. Considering the substantial ecological role that many parasites play in marine communities, fishing and other human impacts could exert cryptic but important effects on marine community structure and ecosystem functioning via reductions in parasite abundance.

Key-words: copepod, isopod, fishing, marine reserves, monogenean, pinnotherid pea crab, trematode

Introduction

Although an estimated 40% of species are parasites (Dobson *et al.* 2008), we have only a limited understanding of how these parasitic species respond to human impacts on ecosystems. As anthropogenic biodiversity loss proceeds, some parasite populations could undergo population decline and extinction (Colwell, Dunn & Harris 2012). Parasites might be even more susceptible to such decline than are free-living species, due to their complex life cycles and dependence on dense populations of hosts for

transmission (Dunn *et al.* 2009; Lafferty 2012). Given the influence of parasites on host populations (Dobson & Hudson 1986; Hudson, Dobson & Lafferty 2006), ecological communities (Minchella & Scott 1991; Combes 1996; Poulin 1999), and whole ecosystems (Lafferty, Dobson & Kuris 2006; Kuris *et al.* 2008), it is critical to understand whether and when environmental change will affect parasite abundance.

In marine ecosystems, fishing is among the most disruptive and long-standing human impacts on biodiversity (Jackson *et al.* 2001; Lotze *et al.* 2006). Because fishing reduces the density of fish, selectively removes large fish and reduces food web complexity, fishing might be

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expected to reduce the efficiency of both direct and indirect parasite transmission, and consequently to lead to a decline in the abundance of fish parasites (Wood, Lafferty & Micheli 2010; and references therein). This pattern has been suggested by one meta-analysis (Ward & Lafferty 2004; see Appendix S1 in Wood, Lafferty & Micheli 2010), one empirical study (Lafferty, Shaw & Kuris 2008) and a comprehensive review of the ecological and parasitological literature (Wood, Lafferty & Micheli 2010).

However, other outcomes are possible (Fig. 1). Specifically, if parasites are resilient to local declines in host abundance due to fishing, they could become concentrated on the hosts that escape fishing (Scenario 1 in Fig. 1). This would increase the abundance of parasites within hosts where hosts are fished, although it would not necessarily result in a greater abundance of parasites overall.

To understand change in parasite populations, two perspectives are necessary. The first – an epidemiological

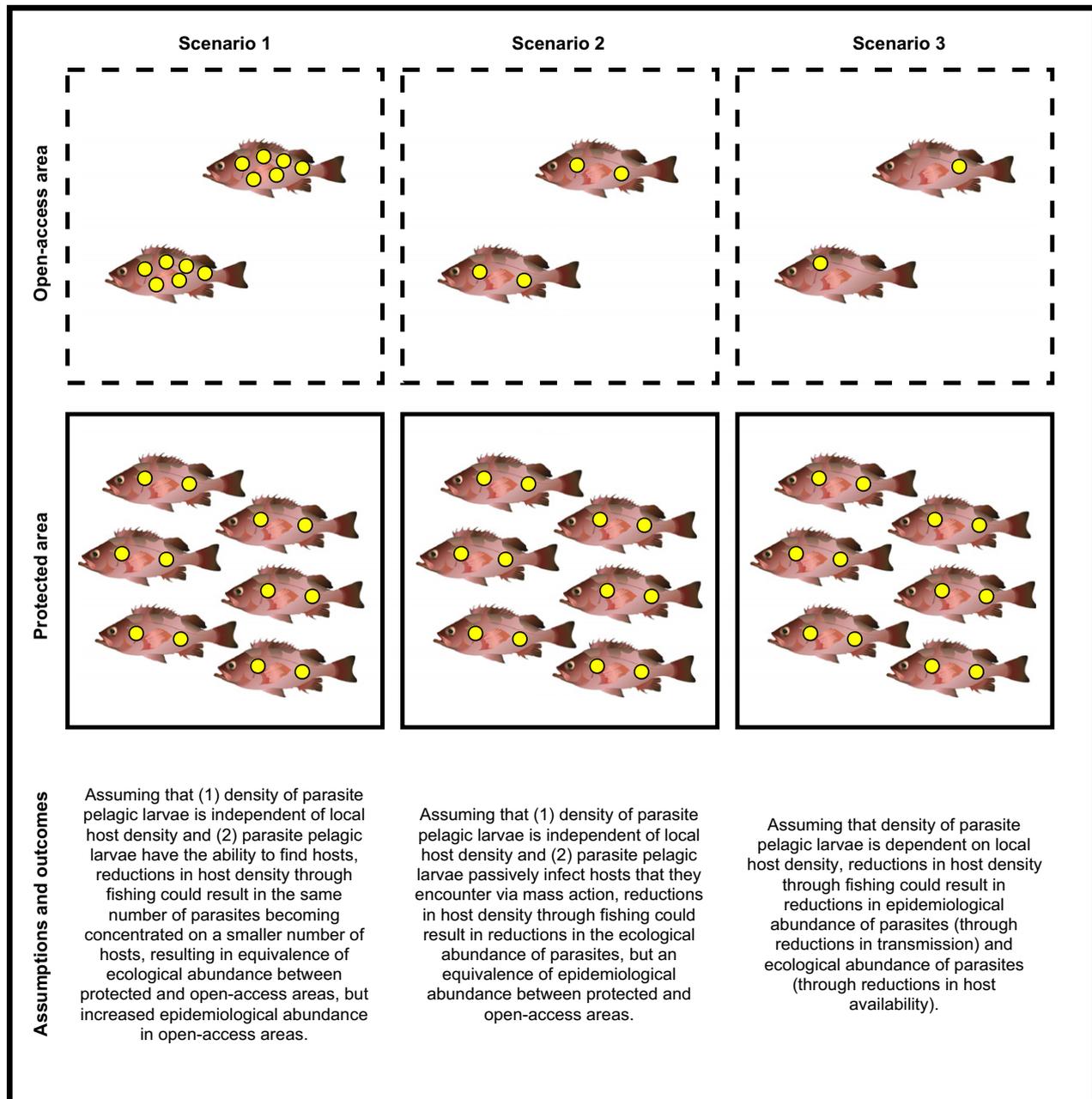


Fig. 1. Conceptual diagram illustrating three alternative hypotheses for the influence of fishing on parasite epidemiological and ecological abundance. Protected areas contain hosts at a higher density than open-access areas. Yellow dots indicate parasites. Images of fish hosts are used for illustrative purposes, but these scenarios also apply to invertebrate hosts. Vector image of fish courtesy of Kim Kraeer and Lucy Van Essen-Fishman, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

approach – quantifies parasites relative to their hosts. Metrics for this approach include prevalence (proportion of hosts infected), intensity (number of parasite individuals per infected host) and ‘epidemiological abundance’, or the number of parasite individuals per host (prevalence * intensity). These are metrics that describe the abundance of parasites within host individuals – that is, they describe the average parasite infrapopulation, or the average group of parasites of a single species that occur in one host individual. Such a perspective is useful for understanding the impact of parasites on hosts and the transmission of parasites among hosts, but it is not necessarily the best way to understand change in parasite abundance. This is because such change does not happen at the level of the parasite infrapopulation, but instead occurs at the larger scale of the parasite population, which includes all parasites of a single species across all host individuals. To address the question of whether parasite populations are increasing or decreasing, the epidemiological approach must be complemented by an ecological one. To differentiate against ‘epidemiological abundance’, we define ‘ecological abundance’ as the number of parasite individuals per host multiplied by the density of hosts, which yields a density of parasites. Density is a unit of measurement used by ecologists in studies of most non-parasitic taxa, but one that is not frequently applied to parasites. Epidemiological and ecological abundances can change in concert or in opposite directions, depending on the nature of the host–parasite interaction, the spatial scale, the presence of alternative hosts and other factors (e.g. Sonnenholzner, Lafferty & Ladah 2011; Fig. 1). We coin the new terms ‘epidemiological abundance’ and ‘ecological abundance’ to highlight the difference between these perspectives, both of which are needed to assess change in parasite populations.

Numerous studies have highlighted the potential for parasites to be extirpated or reduced in abundance by anthropogenic impacts on ecosystems (e.g. Dunn *et al.* 2009; Lafferty 2012). To understand how the ecological abundance metric contributes to assessments of parasite population status and likelihood of parasite extirpation, contrast a parasite with a prevalence of 100%, an intensity of 1, and a rare host (1 host individual per km²) to a parasite with a prevalence of 10%, an intensity of 1, and a common host (100 host individuals per km²). While the first parasite has an ecological abundance of 1 parasite individual per km², the second parasite has an ecological abundance of 10 parasite individuals per km². The parasite with higher prevalence is – counterintuitively – the one more susceptible to extirpation. Tracking ecological abundance therefore helps us to critically assess the status and trajectory of parasite populations. Parasite biomass can be substantial in some ecosystems (Kuris *et al.* 2008; Preston *et al.* 2013), and knowing the overall number of parasites is a first step towards understanding their energetic and ecological role in an ecosystem, and how human impacts might modulate that role.

Several studies have quantified epidemiological metrics of parasite abundance at locations that vary in intensity of fishing pressure, in an effort to understand how fishing might drive change in parasite assemblages. Many of these studies have contrasted marine protected areas and nearby open-access areas, which provides an excellent opportunity to investigate the impacts of fishing, because protected areas tend to modify only fishing impacts, leaving constant local anthropogenic impacts like pollution and global ones like climate change. In our study system in central Chile, a previous investigation of a trematode parasite (*Proctoeces lintoni*) demonstrated greater prevalence among the first intermediate host mussel *Perumytilus purpuratus* and second intermediate host limpet *Fissurella crassa* (Loot, Aldana & Navarrete 2005) and a greater density of infected definitive host fish (Hechinger, Lafferty & Kuris 2008) in two protected areas relative to two nearby open-access areas. Similar studies have been conducted in several Mediterranean marine reserves; for example, greater species richness of trematode parasites was observed among 63 species of teleost fishes (some of which are fished in open-access areas) of the no-take Scandola Nature Reserve relative to similar, open-access areas in the Mediterranean and Black Seas (Bartoli, Gibson & Bray 2005). Higher species richness of all parasites, and higher prevalence of an acanthocephalan parasite (*Acanthocephaloides propinquus*) and several trematodes, was observed in *Gobius bucchichii*, a small benthic fish that is not directly targeted by fishing, of Cerbere–Banyuls, a protected area off the coast of France, relative to nearby, open-access sites (Sasal, Faliex & Morand 1996). In the Balearic Sea, higher species richness of parasites was observed among *Boops boops* in Santa Pola Bay (where the species is rarely fished) than among intensively fished *B. boops* in the Gulf of Oran, and of eight parasite taxa detected, four were more prevalent in the lightly fished area, while one was more prevalent in the heavily fished area (Marzoug *et al.* 2012). In contrast, there was no difference in parasite richness or prevalence among sites with different degrees of protection within the Bonifacio Strait Marine Reserve, despite substantial effects of protection on the host community (Ternengo *et al.* 2009). In the Galapagos, removal of large fish predators reduces predation pressure on crabs that live commensally with sea urchins. Because those crabs eat the eulimid snail parasites of their urchin hosts, the resulting increase in commensal crabs reduces the epidemiological abundance of eulimid snails parasitic on sea urchins in open-access relative to protected areas (Sonnenholzner, Lafferty & Ladah 2011). This variety of results – in which fishing can increase, decrease or not affect parasite abundance – highlights the potential complexity of effects of fishing on parasites.

One important factor that could mediate the response of parasites to the decline of their hosts is the spatial scale of transmission. As is the case for many marine organisms, marine parasite life histories often include a pelagic

larval stage whose dispersal distance is determined by the duration of that life stage – the pelagic larval duration (PLD). The existence of this broadly dispersing infective stage makes space an especially important factor in marine parasite transmission. Transmission of many disease agents is dependent on the density of hosts (e.g. Hochachka & Dhont 2000), and the spatial scale of transmission (i.e. the PLD) should define the area over which host density matters to parasite transmission (e.g. Kuris & Lafferty 1992). That is, for a long PLD parasite, transmission rates or the density of the propagule pool of pelagic larvae will be determined by the density of hosts over a large area and, for a short PLD parasite, transmission rates/propagule pool density will be determined by the density of hosts over a small area, if transmission is density-dependent. In turn, for fishing or protection from fishing to influence parasite transmission, changes in host density must occur at a large spatial scale for a long PLD parasite and need only occur at a small spatial scale for a short PLD parasite. There is a rich literature examining how the interaction of marine reserve size and spacing with PLD influences the recruitment of exploited fish and invertebrates (e.g. Botsford & Hastings 2003; Gaylord *et al.* 2005). Just as large reserves are necessary to conserve exploited species with long pelagic larval durations, whose larvae might otherwise end up outside the protection of the reserve, parasites could respond more strongly to protection of their hosts when that protection occurs at a sufficiently large scale that most parasites produced in the reserve go on to infect hosts in the same reserve.

Here, we describe a study designed to investigate how host infection rates and parasite population sizes respond to protection from fishing. We used a system of marine reserves and matched open-access areas in central Chile as a 'natural experiment', in which we could assess parasite abundance and diversity under fished and unfished conditions while holding other factors constant. We envisioned three potential scenarios for epidemiological and ecological abundance of parasites among exploited hosts from protected versus open-access areas, and these hypotheses are illustrated in Fig. 1. In general, we hypothesized that parasites would attain higher ecological abundance in successful marine reserves, where protection against fishing facilitates dense populations of hosts. However, we also hypothesized that the effect of protection from fishing on epidemiological abundance would be variable and dependent upon parasite traits. Specifically, we expected stronger negative effects of fishing on parasites with shorter PLDs and direct transmission (Scenario 3 in Fig. 1), because those species might be more sensitive to the effects of change in local host density, and because our reserves were small (20–350 ha). We tested these hypotheses by assessing parasite burdens in hosts of four exploited species (two reef fishes and two invertebrates) from three protected and three matched open-access areas. We also assessed host density at all six sites and used this information to calculate parasite ecological

abundance. With this design, we were able to address the questions: (i) how does fishing impact the abundance of parasites within hosts? (ii) how does fishing impact overall parasite populations across hosts? (iii) do responses vary with the life history and ecological characteristics of parasites, specifically PLD?

Materials and methods

STUDY SITES

We chose to perform this study in three of the oldest protected areas of 43 highly successful reserves in Region V, central Chile (Fig. 2). The reserves used in this study were selected because they have been very successful at restoring exploited species (reviewed in Castilla, Gelcich & Defeo 2007; see also Gelcich *et al.* 2008, 2012) and were therefore maximally likely to demonstrate an effect of fishing on parasitism, if present. Our first site is a no-take marine reserve (c. 20 ha; 'Las Cruces') at Estación Costera de Investigaciones Marinas (ECIM), a marine biological laboratory operated by the Pontificia Universidad Católica de Chile (PUC). The reserve at Las Cruces has been closed to the public and to fishers and shellfish collectors since 1982 (Castilla & Duran 1985) and is one of the oldest and best-studied no-take marine reserves in the world, demonstrating dramatic increases in the abundance of exploited species since its establishment (reviewed in Castilla 1999; Castilla, Gelcich & Defeo 2007). Our remaining sites are well-enforced Management and Exploitation Areas for Benthic Resources (MEABRs), in which territorial user rights have been granted to small-scale fishers in defined geographical areas to sustainably manage resources. The management area of Caleta Algarrobo covers 350 ha and has been closed since 1997. The management area of Caleta El Quisco covers 186 ha and has been closed since 1990. Both of these management areas were designated under the Chilean Fisheries and Aquaculture Law (No. 18.892) in 1991 (Castilla, Gelcich & Defeo 2007) and have generated substantial increases in the abundance of exploited species (Gelcich *et al.* 2008, 2012). Each of the three protected areas was matched with a nearby (<7 km apart), open-access site similar in both physical (i.e. wave exposure, substrate type, depth) and biological (i.e. extent of *Lessonia trabeculata* forest) features.

STUDY ORGANISMS

We focused on four exploited species that are both economically important and highly responsive to protection against fishing. Our focal species included two reef fishes (bilagay, *Cheilodactylus variegatus* and jerguilla, *Aplodactylus punctatus*), as well as two invertebrates (the keyhole limpet, *Fissurella latimarginata* and the red sea urchin, *Loxechinus albus*). Along with the muricid gastropod loco (*Concholepas concholepas*), *F. latimarginata* and *L. albus* are among the most economically important benthic fisheries resources in Chile (Castilla, Gelcich & Defeo 2007). While the export market creates most of the demand for the two invertebrate species, local consumption is the primary driver of fishing for *C. variegatus* and *A. punctatus* (Godoy *et al.* 2010). All four species experience substantial increases in abundance in response to cessation or mitigation of fishing pressure (Gelcich *et al.* 2008); specifically, in protected (reserves and management areas) relative to open-access areas, *C. variegatus* is about five times

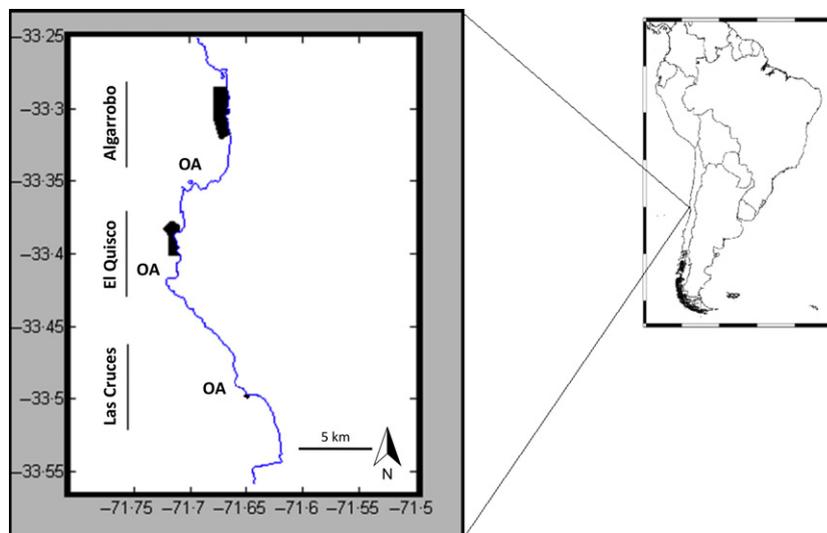


Fig. 2. Map of study area. Shading denotes marine protected areas (site name indicated on left). OA = open-access area.

more dense, *A. punctatus* is about twice as dense, *F. latimarginata* is about six times as dense, and *L. albus* is about 34 times as dense (Gelcich *et al.* 2012).

HOST SAMPLING METHODS

Hosts were collected from each of our six study areas (i.e. three pairs of matched protected and open-access areas) by both scientists and local fishers between August and November 2008 (Table 1). In the two management areas (Algarrobo and El Quisco), fishers collected specimens, but scientists were always present in the fishing boats. We captured invertebrates by hand and fish with spear guns. All specimens were collected at three or more different sites, which were chosen randomly within each study area. All sites were >2 km distant from one another. To maximize body size overlap between specimens collected in protected areas and those collected in open-access areas, we established size categories and attempted to meet collection targets for each size category.

Hosts were processed and preserved immediately following collection. For fish, we measured total length and wet weight and dissected out internal organs. Because the only organs available exclusively for parasitological dissections were the gill arches, we chose to focus only on the gill parasites of the two reef fish species, *C. variegatus* and *A. punctatus*. After dissection, gills were individually wrapped in aluminium foil and frozen for preservation prior to parasitological dissection. For *F. latimarginata*, we measured total length, wet weight and dissected out the gonads. Gonads were individually packaged and frozen for preservation prior to parasitological dissection. For *L. albus*, we measured test diameter, wet weight and emptied the entire test contents into a container for formalin preservation prior to parasitological dissection.

Host density was assessed with three randomly positioned subtidal band transects at each site (see Gelcich *et al.* 2012). All transects were conducted within forests of *Lessonia trabeculata*, in 4–14 m depths. Replicate transects were positioned at least 200 m from one another and were arrayed perpendicular to the coastline. Divers identified and counted all fish and benthic invertebrate observed in 100-m × 2-m belt transects. To minimize

Table 1. Number of hosts dissected for each area (protected or open-access) within each site sampled (Algarrobo, El Quisco and Las Cruces) for two fish hosts and two invertebrate hosts.

Host species	Site	Status	# hosts
<i>Cheilodactylus variegatus</i>	Algarrobo	Protected	22
		Open-Access	17
	El Quisco	Protected	24
		Open-Access	15
	Las Cruces	Protected	20
		Open-Access	2
<i>Aplodactylus punctatus</i>	Algarrobo	Protected	20
		Open-Access	21
	El Quisco	Protected	24
		Open-Access	21
	Las Cruces	Protected	19
		Open-Access	15
<i>Fissurella latimarginata</i>	Algarrobo	Protected	24
		Open-Access	24
	El Quisco	Protected	15
		Open-Access	41
	Las Cruces	Protected	25
		Open-Access	4
<i>Loxechinus albus</i>	Algarrobo	Protected	12
		Open-Access	15
	El Quisco	Protected	44
		Open-Access	22
	Las Cruces	Protected	29
		Open-Access	27

between-observer variability, the same divers performed each transect, with one diver counting only fish and the other counting only invertebrates. Data on host density are presented in Gelcich *et al.* (2012).

PARASITE SAMPLING METHODS

All metazoan parasites present in the preserved host specimens were counted and identified to the lowest possible taxonomic

level. The entire gill arch of fish and the entire gonad of limpets were carefully examined under a stereomicroscope. For urchins, the test contents and formalin preservative were poured into a pan and examined macroscopically for the presence of pea crabs. Where necessary, species identifications were confirmed with taxonomic experts.

For all the parasite taxa we detected, we searched the literature to find estimates of pelagic larval duration (PLD). Because larval development has been studied only for a few widely distributed or commercially important fish parasite species, we inferred the PLD of our species using studies of the most closely related species for which data were available. All species pairs were related at the family level, and many were also in the same genus. We considered each parasite's PLD as the maximum time between hatching and settlement on the host, quantified in laboratory studies as time between hatching and death of the infective stage. This includes the durations of the naupliar and copepodid stages for copepods, the manca stage for cymothoid isopods, the zoeal and megalopal stages for pinnotherid decapods and the oncomiracidial stage for monogenean flatworms. Because gnathiid isopods do not possess a pelagic larval stage (they instead alternate between benthic free-living and ectoparasitic stages throughout the life cycle; Wagele 1988), we did not estimate PLD of this group. We also did not estimate PLD of trematode flatworms because they use up to three distinct host species and have multiple free-living life stages.

STATISTICAL ANALYSIS

For the gill parasite assemblages of *C. variegatus* and *A. punctatus*, we developed rarefaction curves to characterize species richness in each study area by performing resampling of hosts without replacement for 5000 runs in EstimateS (Colwell 2009; after Gotelli & Colwell 2001). We used the nonparametric jackknife estimator to project parasite species richness at the saturation of the species accumulation curve for each host within each study area, calculated using the *SPECIES* package in *R*. To compare jackknife parasite species richness between protected and open-access areas, we ran a mixed-effects general linear model with fishing status (protected versus open-access) and host species (*C. variegatus* and *P. aploactylus*) as fixed effects and site (Algarrobo, El Quisco, and Las Cruces) as a random effect.

To assess whether the epidemiological abundance of parasites differed between protected and open-access areas, we used a mixed-effects generalized linear model with negative binomial error and zero inflation, with fishing status (protected versus open-access) as a fixed factor and site (Algarrobo, El Quisco, Las Cruces) as a random factor. We initially included host body size (measured as total length) as a covariate, but because this predictor was non-significant in all models, we excluded it from final models. With this model, we quantified two metrics of parasite abundance: epidemiological abundance (# of parasites per host) and ecological abundance (density of parasites, or # of parasite individuals per host * density of hosts; data on density of hosts presented in Gelcich *et al.* 2012). Because our ecological abundance metric is a composite of two variables, we performed a simple bootstrapping routine to appropriately propagate the error associated with each component term (Appendix S1). Because many statistical tests were performed, we applied a correction for multiple comparisons to all p-values (false discovery rate or FDR correction; Benjamini & Hochberg 1995).

To check the robustness of our results, we also used a different approach to analyse these data: an unrestricted randomization/permutation procedure. This procedure was run on parasite ecological abundance measured as parasite prevalence (% of hosts infected) and intensity (# of parasites per infected host), as well as on parasite ecological abundance (as above). For detailed methods, see Appendix S1. Qualitative results generally agreed between the two approaches, so the quantitative results from the generalized linear mixed models are reported in this text, and a comparison of the two approaches is reported in Tables S1 and S2.

Results

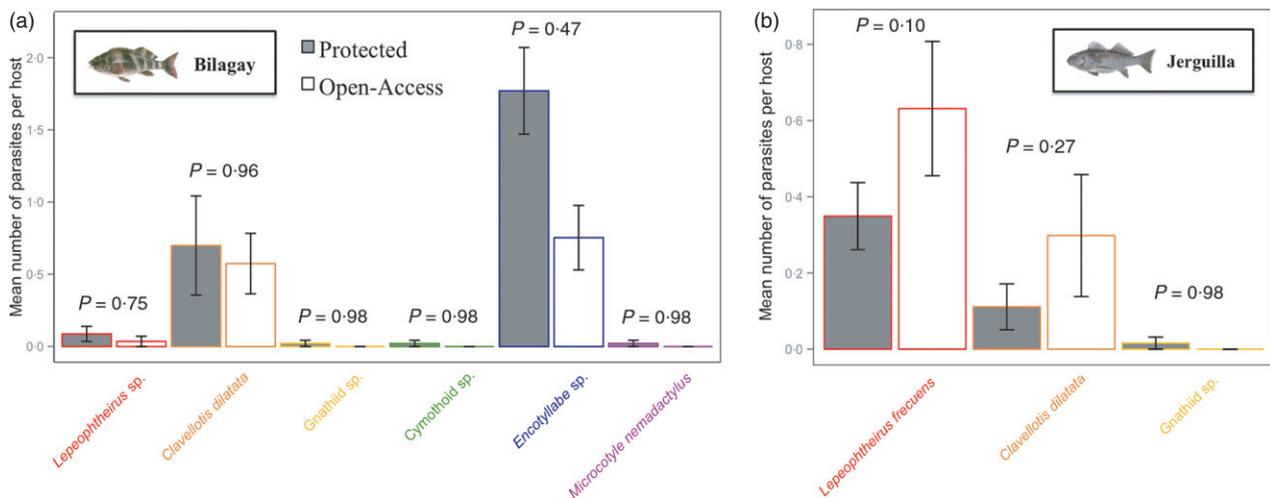
VERTEBRATE HOSTS

We found a total of six parasite taxa on the gills of bilagay (*Cheilodactylus variegatus*) and three on the gills of jerguilla (*Aplodactylus punctatus*; Table 2). Jackknife parasite taxon richness did not differ significantly between protected and open-access areas (mixed-effects general linear model, $t_7 = 1.32$, $P = 0.23$; Figs S1 and S2). Estimated pelagic larval duration varied among the parasite species detected, with the lowest estimated PLDs among the monogenes and the highest among the copepods (Table 2).

We began our analysis of parasite abundance with an assessment of the epidemiological descriptors of the parasite community. In *C. variegatus*, one parasite species, *Encotyllabe* sp., was more abundant within hosts collected from protected areas than in those from open-access areas (GLMM with negative binomial error, $z = 2.45$, d.f. = 70, $p_{\text{raw}} = 0.014$, $p_{\text{corrected}} = 0.047$; Fig. 3a). However, we found that within-host abundance did not differ between protected and open-access areas for *Lepeophtheirus* sp. ($z = 0.75$, d.f. = 70, $p_{\text{raw}} = 0.45$, $p_{\text{corrected}} = 0.75$), *Clavello-tis dilatata* ($z = 0.36$, d.f. = 70, $p_{\text{raw}} = 0.72$, $p_{\text{corrected}} = 0.96$), gnathiid isopods ($z = 0.02$, d.f. = 70, $p_{\text{raw}} = 0.98$, $p_{\text{corrected}} = 0.98$), cymothoid isopods ($z = 0.05$, d.f. = 70, $p_{\text{raw}} = 0.96$, $p_{\text{corrected}} = 0.98$) or *Microcotyle nemadactylus* ($z = 0.02$, d.f. = 70, $p_{\text{raw}} = 0.98$, $p_{\text{corrected}} = 0.98$; Fig. 3a). Gnathiid and cymothoid isopods and *Microcotyle nemadactylus* monogeneans were only found in individuals from protected areas, though in low numbers (Fig. S2). In *A. punctatus*, we found that within-host abundance did not differ between protected and open-access areas for *Lepeophtheirus freuens* ($z = -0.74$, d.f. = 116, $p_{\text{raw}} = 0.035$, $p_{\text{corrected}} = 0.10$), *Clavello-tis dilatata* ($z = -1.55$, d.f. = 116, $p_{\text{raw}} = 0.12$, $p_{\text{corrected}} = 0.27$) or gnathiid isopods ($z = 0.02$, d.f. = 116, $p_{\text{raw}} = 0.98$, $p_{\text{corrected}} = 0.98$; Fig. 3b). As in *C. variegatus*, gnathiid isopod parasites were only observed in *A. punctatus* collected from protected areas, although only one individual was infected (Fig. S2). The mean total length of the fish we collected did not differ between protected and open-access areas for either *C. variegatus* (ANOVA; $F_{1,72} = 1.66$, $P = 0.20$) or *A. punctatus* ($F_{1,118} = 0.66$, $P = 0.42$), and there was no significant relationship

Table 2. Parasite species detected in four hosts collected in central Chile and the estimated pelagic larval duration (Est PLD) of each parasite species. Literature source and taxonomic relatedness of the closely related species used to approximate Est PLD are indicated.

Host	Organ	Parasite class	Parasite family	Parasite species	Est PLD	Source	Relatedness
<i>C. variegatus</i>	Gills	Maxillopoda	Caligidae	<i>Lepeophtheirus</i> sp.	11 days	Pike & Wadsworth (1999)	Genus
		Malacostraca	Lernaeopodidae	<i>Clavellotis dilatata</i>	4 days	Shotter (1971)	Family
			Gnathiidae	Gnathiid sp.	n/a		
			Cymothoidae	Cymothoid sp.	2 weeks	Sandifer & Kerby (1983)	Family
		Monogenea	Capsalidae	<i>Encotyllabe</i> sp.	24 h	Hoshina (1968)	Family
Microcotylidae	<i>Microcotyle nemadactylus</i>	29 h	Remley (1942)	Genus			
<i>A. punctatus</i>	Gills	Maxillopoda	Caligidae	<i>Lepeophtheirus freuens</i>	11 days	Pike & Wadsworth (1999)	Genus
		Lernaeopodidae	Gnathiidae	<i>Clavellotis dilatata</i>	4 days	Shotter (1971)	Family
		Gnathiidae	Gnathiid sp.	n/a			
<i>F. latimarginata</i>	Gonads	Digenea	Fellodistomidae	<i>Proctoeces lintoni</i>	n/a		
<i>L. albus</i>	Intestinal lining	Malacostraca	Pinnotheridae	<i>Pinnaxodes chilensis</i>	16.5 days	Pohle (1989)	Family

**Fig. 3.** Mean number of parasite individuals per host for (a) six species of gill parasites of bilagay (*Cheilodactylus variegatus*) and (b) three species of gill parasites of jerguilla (*Aplocheilichthys punctatus*). Protected areas are shown as shaded columns and open-access areas as white columns. P-values refer to the contrast between protected and open-access areas within parasite taxa and are corrected for multiple comparisons by the FDR method (Benjamini & Hochberg 1995).

between host total length and total parasite burden for either *C. variegatus* ($F_{1,72} = 0.12$, $P = 0.73$) or *A. punctatus* ($F_{1,118} = 0.11$, $P = 0.74$), suggesting that differences between the protected and open-access areas were not due to the effects of host body size.

To obtain measurements of abundance that directly reflect the status of parasite populations, we also assessed the variation in ecological abundance of parasites between protected and open-access areas. In contrast with the epidemiological descriptors, we found that most parasites responded strongly to fishing, with higher ecological abundance in protected than in open-access areas. This was primarily driven by host density, which was five times higher in protected than in open-access areas for *C. var-*

iegatus and twice as high for *A. punctatus* (Gelcich *et al.* 2012). In *C. variegatus*, there were more than three times as many parasites per m^2 for *Clavellotis dilatata* (mean for protected areas = 0.39 parasites m^{-2} ; mean for open-access areas = 0.11 parasites m^{-2} ; GLMM with negative binomial error, $z = 8.38$, d.f. = 998, $p_{raw} < 0.0001$, $p_{corrected} < 0.0001$) and six times as many parasites per m^2 for *Encotyllabe* sp. (mean for protected areas = 1.45 parasites m^{-2} ; mean for open-access areas = 0.24 parasites m^{-2} ; $z = 17.90$, d.f. = 998, $p_{raw} < 0.0001$, $p_{corrected} < 0.0001$; Fig. 4a). Although there were 390 times more parasites per m^2 in protected than in open-access areas for *Lepeophtheirus* sp., due to high variability and the penalty for multiple comparisons, this result was

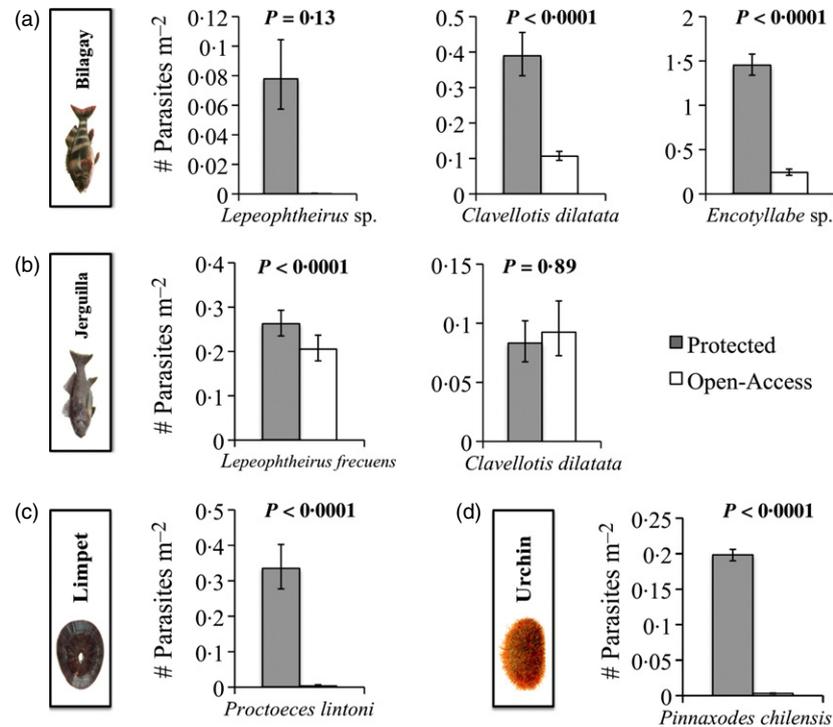


Fig. 4. Ecological abundance (in # of parasites per m²) in protected areas (shaded columns) and open-access areas (white columns) for the bilagay (*Cheilodactylus variegatus*) parasites (a) *Lepeophtheirus* sp., (b) *Clavellotis dilatata*, and (c) *Encotyllabe* sp., the jerguilla (*Aplodactylus punctatus*) parasites (d) *Lepeophtheirus frecuens* and (e) *Clavellotis dilatata*, (f) the keyhole limpet (*Fissurella latimarginata*) parasite *Proctoeces lintoni*, and (g) the red sea urchin (*Loxechinus albus*) parasite *Pinnaxodes chilensis*. Shown are bootstrap means and error bars reflecting the 95% approximate bootstrap confidence interval (ABC or approximate BC_a method, after Efron & Tibshirani 1993). P-values refer to the contrast between protected and open-access areas within parasite taxa and are corrected for multiple comparisons by the FDR method (Benjamini & Hochberg 1995).

not significant (mean for protected areas = 0.08 parasites m⁻²; mean for open-access areas = 0.0002 parasites m⁻²; $z = 1.94$, $p_{\text{raw}} = 0.05$, $p_{\text{corrected}} = 0.13$). In *A. punctatus*, there were 28% more parasites per m² in protected than in open-access areas for *Lepeophtheirus frecuens* (mean for protected areas = 0.26 parasites m⁻²; mean for open-access areas = 0.21 parasites m⁻²; $z = 5.32$, d.f. = 998, $p_{\text{raw}} < 0.0001$, $p_{\text{corrected}} < 0.0001$), but no difference between protected and open-access areas for *Clavellotis dilatata* (mean for protected areas = 0.08 parasites m⁻²; mean for open-access areas = 0.09 parasites m⁻²; $z = 0.24$, d.f. = 998, $p_{\text{raw}} = 0.62$, $p_{\text{corrected}} = 0.89$; Fig. 4b).

INVERTEBRATE HOSTS

We found one parasite species (the trematode *Proctoeces lintoni*) in the gonad of *Fissurella latimarginata* and one (the parasitic pinnotherid pea crab, *Pinnaxodes chilensis*) in the test cavity of *Loxechinus albus* (Table 2). For both hosts, infected individuals tended to be larger than uninfected individuals (*F. latimarginata*: ANOVA, $F_{1,131} = 5.34$, $P = 0.02$; *L. albus*: $F_{1,147} = 2.67$, $P = 0.10$). This pattern often holds for hosts with parasitic infections that persist for long periods of time and in which size is correlated with age, as older and larger hosts tend to have

accumulated more parasites. Furthermore, average body size of hosts collected for dissection was significantly greater in protected than in open-access areas for both *F. latimarginata* (ANOVA, $F_{1,131} = 77.61$, $P < 0.0001$) and *L. albus* ($F_{1,147} = 9.58$, $P = 0.002$; Fig. S3). We accounted for the influence of host body size on parasite prevalence by including body size as a covariate in all analyses. For *F. latimarginata*, the within-host abundance of the trematode *Pr. lintoni* did not differ between protected and open-access sites after controlling for host body size (GLMM with negative binomial error, effect of protection status: $z = -1.39$, d.f. = 128, $p_{\text{raw}} = 0.16$, $p_{\text{corrected}} = 0.32$; effect of body size: $z = 1.28$, d.f. = 128, $p_{\text{raw}} = 0.20$, $p_{\text{corrected}} = 0.36$; Fig. S4). Similarly, the pinnotherid pea crab parasite *Pi. chilensis* in *L. albus* was present at a very high (mean = 85%, range = 67–100%) and roughly equivalent prevalence across protected and open-access sites (effect of protection status: $z = -0.11$, d.f. = 146, $p_{\text{raw}} = 0.91$, $p_{\text{corrected}} = 0.98$), regardless of the effect of body size ($z = 0.56$, d.f. = 146, $p_{\text{raw}} = 0.58$, $p_{\text{corrected}} = 0.88$; Fig. S4).

We also calculated the ecological abundance of both *Pr. lintoni* and *Pi. chilensis* using the same method employed for the two vertebrate hosts. As we observed for the parasites of the vertebrate hosts, we found that both *Pr. lintoni* and *Pi. chilensis* responded strongly to relaxation of fishing pressure, with higher ecological abun-

dance in protected than in open-access areas. This was primarily driven by host density, which was six times higher in protected than in open-access areas for *F. latimarginata* and 34 times higher for *L. albus* (Gelcich *et al.* 2012). In *F. latimarginata*, there were, on average, 97 times more *Pr. lintoni* in protected than in open-access areas (mean for protected areas = 0.34 parasites m⁻²; mean for open-access areas = 0.004 parasites m⁻²; GLMM with negative binomial error, $z = 5.97$, d.f. = 998, $p_{\text{raw}} < 0.0001$, $p_{\text{corrected}} < 0.0001$; Fig. 4c) and more than 66 times more *Pi. chilensis* in protected than in open-access areas (mean for protected areas = 0.20 parasites m⁻²; mean for open-access areas = 0.003 parasites m⁻²; $z = 5.13$, d.f. = 998, $p_{\text{raw}} < 0.0001$, $p_{\text{corrected}} < 0.0001$; Fig. 4d).

Discussion

Our study demonstrates that protection against fishing facilitates parasite populations and can, in certain cases, facilitate parasite infrapopulations. We found a statistically significant epidemiological effect of marine protected areas for only one of the eleven total parasite species detected in this study (*Encotyllabe* sp. from the gills of *Cheilodactylus variegatus*; Scenario 3 in Fig. 1), whereas the remaining ten species displayed no significant differences in prevalence or intensity between protected and open-access areas (Scenario 2 in Fig. 1). However, the responsive species was the one with the shortest pelagic larval duration (PLD), suggesting that the spatial scale of transmission might mediate the response of parasite transmission rates and epidemiological abundance to local-scale changes in host density (Fig. 1). On the other hand, all species but two (*Lepeophtheirus* sp. from the gills of *Cheilodactylus variegatus* and *Clavellotis dilatata* from the gills of *Aplodactylus punctatus*) were found at higher ecological abundances in protected relative to open-access areas. We never observed significantly higher parasite epidemiological or ecological abundance in open-access relative to protected areas (Scenario 1 in Fig. 1). We interpret these findings as evidence that overall parasite population sizes are depressed by the removal of hosts via fishing. These results also hint that protection from fishing might increase the prevalence and intensity of parasites on exploited marine species provided that the scale of protection matches or exceeds the scale of parasite transmission.

Of the nine fish gill parasite taxa detected, five were observed more than once and were therefore amenable to investigations of their epidemiological abundance (in *C. variegatus*, the copepods *Lepeophtheirus* sp. and *Clavellotis dilatata* and the monogenean *Encotyllabe* sp.; in *A. punctatus*, the copepods *Lepeophtheirus frekuensi* and *Clavellotis dilatata*). Copepod and monogenean parasites of fish proceed through two general phases of development: juvenile and adult life stages that are ectoparasitic on fish hosts and a free-living larval stage that disperses

from the parent's host to a new host individual. For copepods, the free-living larval nauplius and copepodid stages are relatively long-lived (persisting for four to 11 days in laboratory conditions; Table 2), but for monogeneans, the free-living oncomiracidium is short-lived (persisting for approximately 1 day in laboratory conditions; Table 2). With this short estimated PLD, transmission of *Encotyllabe* sp. might be more dependent upon local parasite reproduction – and therefore more responsive to local reductions in host abundance (Scenario 3 in Fig. 1) – than is transmission of parasites with longer dispersal durations and resulting dispersal distances (Scenario 2 in Fig. 1). Our reserve and open-access areas are small: the biggest is 350 hectares, which may be too small to encompass the scale of transmission of parasites with longer estimated PLDs (e.g. copepods), whose populations are subsidized by inputs of larvae from distant areas. The importance of scales of dispersal relative to the scale of protection has been highlighted in modelling studies of marine reserve efficacy in enhancing populations of fish and invertebrates targeted by fishing (Botsford & Hastings 2003; Gaylord *et al.* 2005) and in mathematical models of the parasites of exploited crustaceans (Kuris & Lafferty 1992). The effective scale of dispersal of parasites should be affected by host movement as well, but this would apply equally to all parasites within a single host species and does not explain divergence between *Encotyllabe* sp. and the other gill parasite species in *C. variegatus*. The interaction between parasite PLD and scale of protection might be reinforced by the extreme host specificity of monogeneans (Sasal, Desdevises & Morand 1998). Because parasites with broader host ranges (like copepods) are able to rely on alternate host species, their transmission rates might be less tightly coupled to the density of an exploited host and, therefore, less strongly influenced by protection status than would be the case for the host-specific monogeneans.

Mismatch between scales of parasite dispersal and marine protected area size might also explain why we observed no epidemiological patterns for the sea urchin parasite, *Pinnaxodes chilensis*, or the limpet parasite, *Proctoeces lintoni*. *Pi. chilensis* has a long estimated PLD (>2 weeks; Table 2), and this might have rendered the parasite's transmission rates insensitive to the small-scale changes in host density driven by our small marine protected areas. Note that this pattern could also be explained by saturation of hosts, as *Pi. chilensis* attained 100% prevalence at some sites. *Pr. lintoni*, a trematode parasite, differs from the remaining parasite taxa detected in this study in that it possesses a complex life cycle involving multiple host species. This might increase the effective scale of its estimated PLD, as the degree to which larval parasites infecting limpets disperse from their natal site will be determined by dispersal of the pelagic larval stage (i.e. the cercaria), the benthic larval stage (i.e. the miracidium), as well as the vertebrate definitive host (a clingfish, *Sicyases sanguineus*).

The hypothesis that varying dispersal abilities might drive some similarities and differences among results in this and other studies (e.g. Sasal, Faliex & Morand 1996; Bartoli, Gibson & Bray 2005; Loot, Aldana & Navarrete 2005; Ternengo *et al.* 2009; Marzoug *et al.* 2012) needs to be further explored through empirical work and mathematical modelling. But, if the epidemiological response of parasites to protection against fishing is, as we propose, dependent upon the scale of protection, larger marine protected areas could produce epidemiological increases in parasite species with longer PLDs (i.e. increasing the scale of protection could encompass the spatial scale of transmission of increasingly longer-PLD parasites, shifting them from Fig. 1's Scenario 2 into Scenario 3). Thus, we would expect an increasing proportion of parasite species to exhibit responsiveness to protection with increasing size of reserves. If we consider that fishing affects large areas of ocean habitat (Halpern *et al.* 2008), it seems likely that many marine parasite assemblages have experienced fishing of sufficient spatial extent to encompass the scale of transmission of most marine fish parasites.

Regardless of whether a parasite species responded to protection with an increase in epidemiological abundance, almost all were more ecologically abundant in protected than in open-access areas, sometimes by orders of magnitude. Ecological abundance was calculated by multiplying the density of fish hosts by the number of parasite individuals per host. Because the second term in the equation for the calculation of ecological abundance is functionally epidemiological (i.e. describes the abundance of parasites per host), and we know that epidemiological parameters were similar between protected and open-access areas (for all species other than *Encotyllabe* sp.), the primary driver of the differences in ecological abundance is the density of hosts, although small, non-significant differences in epidemiological abundance also contribute. Therefore, our data suggest that greater availability of hosts facilitates a greater overall abundance of parasites, but does not necessarily increase rates of transmission of parasites among hosts. At first blush, this may seem to provide an example in which transmission is not density-dependent, but it is more likely that the scale of observation does not match the scale of density dependence – that is, because many of these parasites possess long PLDs, their transmission rates might be set at scales that exceed the size of our study areas.

Because ecological abundance is the metric that best reflects the population status of parasites species, our data suggest that fishing can reduce parasite population sizes. While many might consider a reduction in parasite abundance to be beneficial, the loss of parasites from ecosystems is likely to have negative ecological effects (reviewed in Gomez, Nichols & Perkins 2012). For example, parasites can constitute a large proportion of total community biomass – sometimes matching or exceeding the biomass of predators (Kuris *et al.* 2008; Preston *et al.* 2013). Change in overall parasite populations might

therefore have substantial effects on energy flow through ecosystems. More importantly, parasites constitute at least 40% of species on the planet (Dobson *et al.* 2008). Loss of parasites therefore represents a threat to a large proportion of global biodiversity. At the very least, our understanding of global biodiversity is incomplete without consideration of how human impacts affect parasite populations.

We sought to use marine protected areas in a natural experiment to understand how fishing drives change in parasite assemblages. This approach allows us to work at spatial scales that would be impractical to manipulate experimentally, but it must be borne in mind that our reserves are imperfect for this purpose in several ways: (i) they have been fished intensively in the past and have only recently (within the past 10–30 years) been restored, (ii) some of these reserves still experience substantial fishing pressure, even though this fishing is heavily regulated, and (iii) in general, trajectories of recovery may not match trajectories of decline, leading to mismatches between unfished (i.e. never fished) and fully restored states. These caveats suggest that reserves are not ideal representations of unfished marine ecosystems, but if anything, they probably underestimate the ecological differences between fished and unfished states.

Our study demonstrates that fishing drives reductions in the ecological abundance of the parasites of exploited hosts and suggests that fishing may also drive reductions in parasite epidemiological abundance, if the spatial scale of protection matches or exceeds the spatial scale of transmission. The latter finding highlights the potential significance of spatial scale in mediating the influence of human impacts on marine parasite transmission dynamics. These new insights lend support to the hypothesis that parasites of exploited marine species may have been more abundant prior to the advent of large-scale fishing impacts on ocean ecosystems and suggest a novel function for marine protected areas: parasites comprise a substantial proportion of the Earth's species, so in promoting conservation of fish hosts, marine reserves appear to also contribute to the conservation of the large segment of global biodiversity that is parasitic.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detailed statistical methods

Table S1. Side-by-side comparison of results from two approaches to analysing differences in parasite epidemiological abundance between protected and open-access areas.

Table S2. Side-by-side comparison of results from two approaches to

analysing differences in parasite ecological abundance between protected and open-access areas.

Figure S1. Observed parasite species accumulation curves for *Cheilodactylus variegatus* and *Aplodactylus punctatus* collected from protected and open-access areas

Figure S2. Mean jackknife estimates of parasite species richness and 95% confidence intervals for *C. variegatus* and *A. punctatus* parasites in reserves and open-access areas and table of overall parasite community taxon richness

Figure S3. Prevalence (% of hosts infected) for *Proctoeces lintoni* in *Fissurella latimarginata* and *Pinnaxodes chilensis* in *Loxechinus albus* in open-access and protected areas